Hippoporidra edax (Busk 1859) and a revision of some fossil and living *Hippoporidra* (Bryozoa)

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Synopsis

Hippoporidra edax, the type species of *Hippoporidra* Canu & Bassler 1927, has been revised following a study of type and other specimens from the Pliocene Coralline Crag of Suffolk. Recent British bryozoans previously referred to *H. edax* are considered to be a distinct species, *H. lusitania* sp. nov. This and four established species of *Hippoporidra* are distinguished by a key which uses the form of the interzooidal avicularium and the shape of the autozooidal orifice. Miocene and Pliocene fossil populations of *H. edax* from Europe compare closely with some living populations from the western Atlantic but differ from the four recognizable living species of *Hippoporidra* from the eastern Atlantic.

Introduction

The first major publication on British fossil bryozoans was George Busk's monograph of bryozoans from the Pliocene and Pleistocene Crags of East Anglia, published in 1859. Busk's type material is now in the palaeontological collections of the British Museum (Natural History). This includes specimens of a particularly interesting cheilostome, *Cellepora edax* Busk 1859, which was subsequently designated as the type species of *Hippoporidra* by Canu & Bassler (1927). Several Recent and fossil species have been referred to *Hippoporidra*, including supposed living examples of *H. edax*. The major objective of this paper is to present a systematic revision of *H. edax*, based on a study of type and additional specimens from the Pliocene Coralline Crag, and to explore its implications for fossil and Recent species of *Hippoporidra*.

All described material is housed in either the palaeontological or zoological collections of the British Museum (Natural History).

Historical review

Early interest in *H. edax* focussed on the relationship between the bryozoan and the host substrate, always a gastropod shell. Busk (1859) believed *H. edax* to be a parasite of the gastropod because, although the shape of the bryozoan colonies he studied (Fig. 1) attested to their origin as gastropod associates, he could rarely find any trace of the original gastropod shell. This, he thought, was because the bryozoan was a shell-dissolving parasite of the gastropod. Hincks (1862), working on Recent *Hippoporidra*, agreed with Busk that the bryozoan had the ability to dissolve its shell substrate, later adding (Hincks 1880 : 313) that the bryozoan zoarium 'supplies a good and solid substitute for the house which it has supplanted'. Although Wood (1872 : 55) also suspected *H. edax* to be a parasite of

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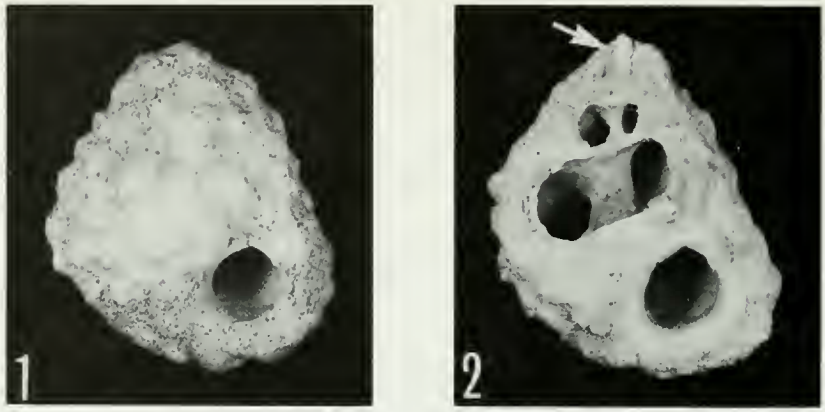

Figs 1, 2 *Hippoporidra edax* (Busk). Coralline Crag, Suffolk. Fig. 1, lectotype B1620, showing typical thick encrustation developed on a gastropod shell; ×2·5. Fig. 2, 23459a, fractured specimen showing helicospiral chamber constructed by bryozoan colony growth and the tiny gastropod shell substrate (arrowed); × 2·5.

gastropods, he thought that the gastropod destroyed its own shell, 'in order to lighten its heavy and inconvenient incumbrance'.

It is now known that most colonies of *Hippoporidra* are associates not of living gastropods but of hermit crabs which occupy empty gastropod shells (e.g. Cook 1964, 1968). Bryozoan growth during pagurid tenancy mimics gastropod shell growth by forming a helicospiral coil originating at the aperture of the gastropod shell. Helicospiral bryozoan growth is presumably a direct result of the presence of a pagurid whose curved body, adapted to fit a helicospiral gastropod shell, acts as a template around which the bryozoan grows. The original gastropod shell substrate may be left deeply embedded within the apex of the bryozoan colony (Fig. 2). This explains why Busk was rarely able to locate the original gastropod shell and why he was misled into believing that *H. edax* was a shell-dissolving parasite. It should, however, be noted that some bryozoans have the capacity to etch calcareous substrates (Pinter Morris 1975) or to bore into them (Pohowsky 1978).

Busk (1859) further commented on the likeness between the 'basal lamina' of *H. edax* (i.e. the wall lining the helicospiral pagurid living chamber) and the undersurface of *Lunulites* colonies. The basal wall in the free-living bryozoan *Lunulites* is now known to be an interior wall (*sensu* Boardman & Cheetham 1973) consisting of a calcified layer which accreted beneath a cover of hypostegal coelom (Håkansson 1973). The presence of a chamber-lining interior wall (Fig. 6b, p. 249) has been recently established in *Hippoporidra* and its formation and role in the development of *Hippoporidra* colonies will be discussed elsewhere (Cook & Taylor, in preparation).

Systematic descriptions

Order CHEILOSTOMATA

Suborder ASCOPHORA

Family CLEIDOCHASMATIDAE Cheetham & Sandberg, 1964

Genus *HIPPOPORIDRA* Canu & Bassler, 1927

[*Hippoporidra* Canu & Bassler, 1927 : 8; Canu & Bassler 1929 : 418; Osburn 1940 : 454; Osburn 1952 : 354; Lagaaij 1952 : 147; Buge 1957 : 320; Cook 1964 : 22; Cook 1968 : 196; Pouyet 1973 : 54 (*partim*); Hayward & Ryland 1979 : 214; Cook in press].

DESCRIPTION. Colony generally encrusting pagurid-tenanted gastropod shells, multilamellar,

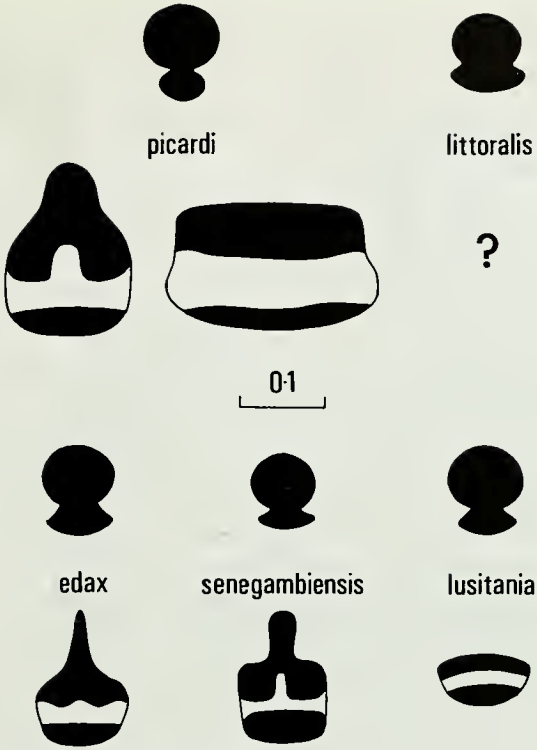

Fig. 3 Shape of the autozooidal orifice and rostrum of the interzooidal avicularium in five species of *Hippoporidra*. Interzooidal avicularia were not located in studied specimens of *H. littoralis*. Scale bar is 0·1 mm.

monticulate and occasionally branched. Autozooids with marginal pores and scattered or absent frontal pores. Calcified frontal shields cryptocystidean, with overlying hypostegal coelom. Orifice cleithridiate with strong lateral condyles; oral spines absent. Most autozooids are frontally-budded between monticules and are irregularly shaped. Cortical zooids, situated on monticules, are larger than autozooids but have a smaller orifice. Ovicells are hyperstomial, imperforate, with an uncalcified frontal area, and are not closed by the operculum. Avicularia are small and adventitious or large and interzooidal.

TYPE SPECIES. *Cellepora edax* Busk 1859, by original designation; Pliocene, Suffolk.

REMARKS. Using established correlates of character states of orifice shape and avicularian skeletal morphology (cf. Hayward 1978), five species of *Hippoporidra* may be recognized (see key below and Fig. 3): *H. edax* (Busk), *H. lusitania* sp. nov., *H. littoralis* Cook, *H. picardi* Gautier and *H. senegambiensis* (Carter). The only species known as a fossil is *H. edax* and this is present in deposits of the early Miocene onwards. Living North American species of *Hippoporidra* are inadequately known and, in addition to probable *H. edax*, include some undescribed species.

Lepralia edax forma *janthina* Smitt 1873 was formerly regarded as *Hippoporidra janthina* (Smitt) but has since been shown to be a species of *Hippotrema* (Cook in press).

KEY to species of *Hippoporidra* (see Fig. 3).

1. Narrow rounded poster; interzooidal avicularia with either broad (simple pivotal bar) or pear-shaped (ligulate pivotal bar) rostra . . . . . ***H. picardi***

– Broad poster, wider than anter; interzooidal avicularia absent or rare . . . . *H. littoralis*
– Broad poster, the same width as or slightly narrower than anter 2

2. Interzooidal avicularium with pointed rostrum and doubly constricted pivotal bar . . . . . *H. edax*
– Interzooidal avicularium with spatulate rostrum and ligulate pivotal bar . . *H. senegambiensis*
– Interzooidal avicularium with transversely elliptical rostrum and simple pivotal bar *H. lusitania*

Hippoporidra edax (Busk, 1859)

? 1847 *Cellepora parasitica* Michelin : 326; pl. 78, fig. 3.
1859 *Cellepora edax* Busk : 59; pl. 9, fig. 6; pl. 22, fig. 3.
non 1859 *Cellepora parasitica* Michelin; Busk : 61; pl. 9, figs 11, 13 [= *Osthimosia parasitica*].
1872 *Cellepora edax* Busk; Wood : 54; pl. 5, fig. 25.
1873 *Lepralia edax* forma *calcarea* Smitt : 63; pl. 11, figs 220–223.
non 1873 *Lepralia edax* forma *janthina* Smitt : 63; pl. 11, figs 224–225 [= *Hippotrema janthina*].
? 1904 *Lepralia maculata* Ulrich & Bassler : 423; pl. 115, figs 8, 9; pl. 118, fig. 7.
1912 *Cellepora edax* Busk; Leriche : 805, text-figs 41, 41a, 42, 42a.
1923 *Cellepora minuta* Canu & Bassler : 182; pl. 25, figs 10–13.
? 1923 *Cellepora maculata* (Ulrich & Bassler) Canu & Bassler : 182; pl. 25, figs 14–20.
1924 *Cellepora edax* Busk; Duvergier : 186; pl. 6, figs 5–10.
1928 *Hippoporidra edax* (Busk); Canu & Bassler : 139; pl. 22, figs 1–4.
1928 *Hippoporidra calcarea* (Smitt); Canu & Bassler : 140; pl. 22, figs 5, 6; text-fig. 30.
1929 *Hippoporidra calcarea* (Smitt); Canu & Bassler : fig. 163 C–H.
? 1948 *Cellepora parasitica* Michelin; Roger & Buge : 461; pl. 17, figs 1, 4–7, 10–13.
? 1948 *Hippoporidra edax* (Busk); Roger & Buge : 465; pl. 17, figs 8, 9.
1949 *Hippoporidra edax* (Busk); Vigneaux : 81, fig. 32.
1952 *Hippoporidra edax* (Busk); Lagaaij : 147; pl. 15, fig. 13; pl. 16, fig. 6.
1957 *Hippoporidra edax* (Busk); Buge : 320; pl. 12, figs 3–6 only [pl. 11, fig. 2 = *H. senegambiensis*].
? 1962 *Cellepora parasitica* Michelin; Buge & Lecointre : pl. 18, figs 1, 5 only [pl. 18, fig. 2 = *H. senegambiensis*].
1964 *Hippoporidra edax* (Busk); Cook : 26 (*partim*); pl. 3, fig. 7 only.
1973 *Hippoporidra edax* (Busk); Pouyet : 120; pl. 2, figs 4–6; pl. 13, fig. 1; pl. 16, fig. 2.

Revised diagnosis. Autozooid orifice with poster slightly narrower than anter; interzooidal avicularium with an acute rostrum and doubly constricted pivotal bar.

Lectotype (designated by Lagaaij 1952). BM(NH) Palaeontology Dept. no. B1620; Coralline Crag, Sudbourne, Suffolk (Busk 1859 : pl. 9, fig. 6a–c).

Material. All Coralline Crag of Suffolk: 23459a–d, Sudbourne, Daniels Coll.; 60338a–b, Sutton, Bell Coll.; 60463a–b, Butley River Marshes; 60475a–c, 60477, Boyton, Charlesworth Coll.; B1012a–b, Gedgrave, Tennant Coll.; D6699, D6700–2, D6704–6, D6755, D6756 (? Busk 1859 : pl. 22, fig. 3c), D6757, D6758a–b, D6759 (? Busk 1859 : pl. 22, fig. 3b), D6761 (? Busk 1859 : pl. 22, fig. 3a), D6767, Wood Coll.; D52744, near Orford Castle; G3967 (Wood 1872 : pl. 5, fig. 25a), near Orford, Wood Coll.

Recorded occurrence. Miocene of France (Loire, Aquitaine) and the eastern U.S.A.; Pliocene of England (Suffolk), France, Italy (Valle Botto), Belgium, Holland and the eastern U.S.A.; Recent of the east coast of the U.S.A. and the Gulf of Mexico.

Description. Colonies monticulate (Fig. 1), multilamellar, exclusively encrusting gastropod shells. Autozooids (Figs 4B, 5a) with marginal pores, some frontal pores, suboral area imperforate and sometimes developed as an umbo. Orifice with strong lateral condyles dividing a poster from a slightly broader, rounded anter. Cortical zooids (Figs 4A, 5c) umbonate, larger than autozooids with a slightly smaller orifice. Adventitious avicularia (Fig. 4B) acute, small. Interzooidal avicularia rostra (Fig. 5b) broad proximally with a doubly constricted pivotal bar, narrow terminally and acute. Ovicells (Fig. 5d) rounded with a frontal area.

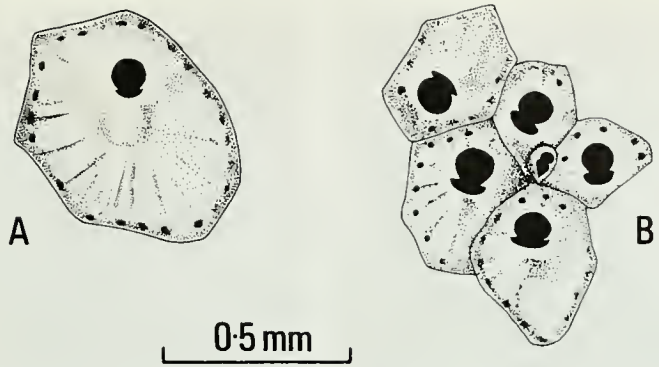

Fig. 4 *Hippoporidra edax* (Busk). Coralline Crag, Suffolk. A, cortical zooid drawn from the lectotype B1620; B, irregularly-shaped, frontally-budded autozooids and an adventitious avicularium drawn from specimen 23459b.

DIMENSIONS. Autozooid orifice length 0·10–0·11 mm, width 0·07–0·08 mm; cortical zooid orifice length 0·09–0·10 mm, width 0·07 mm; interzooidal avicularium rostrum length 0·15–0·17 mm, width 0·13–0·14 mm.

REMARKS. Michelin's (1847) type specimens of *Cellepora parasitica* are apparently lost (Roger & Buge 1948) and neither his figure nor his description are sufficient to permit positive identification of the species. The *Cellepora parasitica* Michelin of Busk (1859) may not be the same species as that described by Michelin. It has been redescribed by Lagaaij (1952) under the name *Osthimosia parasitica* (Busk, ? *non* Michelin).

Specimens of the N. American species *Cellepora minuta* Canu & Bassler (1923) in the collections of the BM(NH) confirm its synonymy with *H. edax*. The closely similar *Lepralia maculata* Ulrich & Bassler (1904) may be also a junior synonym.

Lepralia edax forma *calcarea* Smitt 1873, described from the Recent of Florida, has interzooidal avicularia identical with those of Coralline Crag *H. edax*, suggesting its synonymy.

Hippoporidra lusitania sp. nov.

1861 *Cellepora edax* Busk; Busk : 154, figs 3, 3a.
1862 *Cellepora edax* Busk; Hincks : 304.
1880 *Lepralia edax* (Busk) Hincks : 311 (*partim*); pl. 24, figs 7, 8 only [fig. 7a = *H. edax*].
1929 *Hippoporidra edax* (Busk); Canu & Bassler : fig. 163A, B.
1937 *Lepralia edax* (Busk); Moore : 202.
1964 *Hippoporidra edax* (Busk); Cook : 26 (*partim*); pl. 3, figs 5, 6 only.
1979 *Hippoporidra edax* (Busk); Hayward & Ryland : 214, fig. 91A–E.

DIAGNOSIS. Autozooid orifice with poster slightly narrower than anter; interzooidal avicularium with a transversely elliptical rostrum and a simple pivotal bar.

HOLOTYPE. BM(NH) Zoology Dept. no., 1911.10.1.1143a; Guernsey, Norman Coll.

PARATYPES. 1899.5.1.1517a–b, Plymouth, Hincks Coll.; 1899.7.1.1410, Coast of Devon, Busk Coll. (? Busk 1861 : figs 3, 3a); 1899.7.1.1410A, Guernsey ?, Busk Coll.; 1911.10.1.1143 b–i, Guernsey, Norman Coll.; 1963.3.30.273, Scilly Isles (35 fathoms), Buskill Coll.; 1963.4.16.1, ? Guernsey, Busk Coll. All BM(NH) Zoology Dept. numbers.

DISTRIBUTION. Recent of British coastal waters. Hayward & Ryland (1979) record the species from the Isle of Man, the western English Channel, the Scilly Isles, the north and south coasts of Devon and Cornwall, and also the Gulf of St Malo.

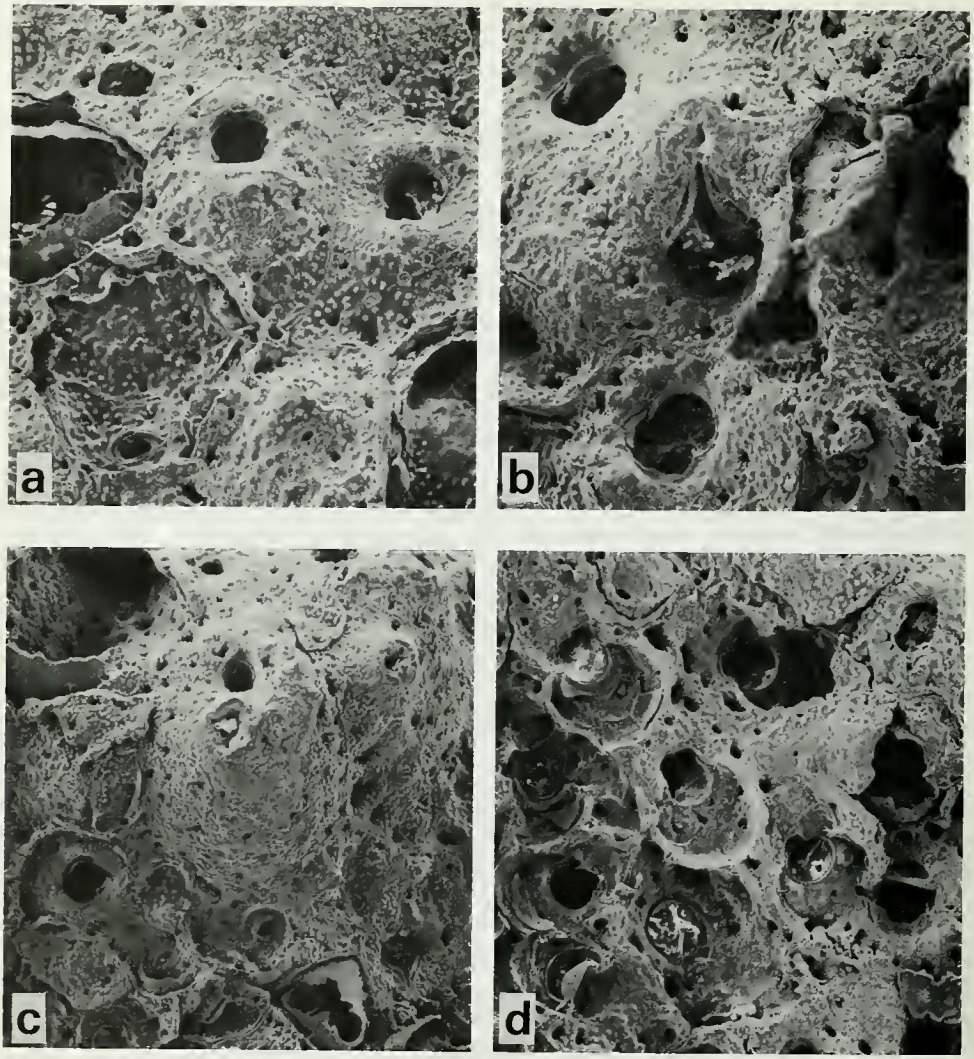

Fig. 5 *Hippoporidra edax* (Busk). Coralline Crag, Suffolk. Scanning electron micrographs of specimen 23459c. a, autozooids and a frontal bud (bottom left), ×90. b, interzooidal avicularium, ×110. c, cortical zooid with broken umbo, ×60. d, ovicelled zooids with frontal part of ovicell wall missing and basal wall penetrated by septulae, ×80.

DESCRIPTION. Colonies monticulate, multilamellar, exclusively encrusting gastropod shells inhabited by pagurids. Autozooids (Fig. 6c) with marginal and some frontal pores; suboral area imperforate, variably umbonate. Cortical zooids (Fig. 6a) large but with orifice distinctly smaller than that of autozooids. Adventitious avicularia (Fig. 6d) ovate, small. Interzooidal avicularia (Fig. 3) with a transversely elliptical rostrum and a simple, curved pivotal bar. Ovicells (Fig. 6d) rounded to semi-ovoid with a distally-placed frontal area.

DIMENSIONS. Autozooid orifice length 0·09–0·10 mm, width 0·07–0·08 mm; cortical

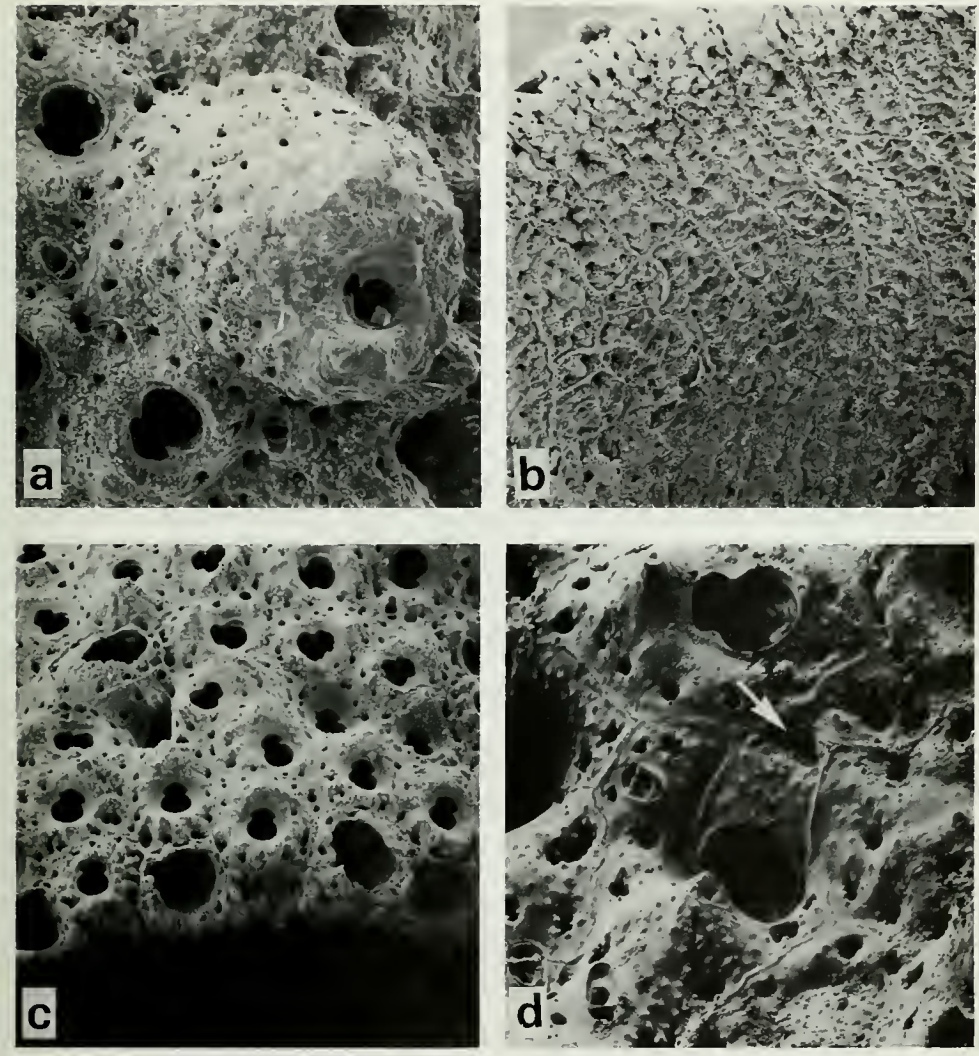

Fig. 6 *Hippoporidra lusitania* sp. nov. Recent, Guernsey. Scanning electron micrographs of **holotype,** 1911.10.1.1143a. a, cortical zooid, autozooids and small adventitious avicularia, × 100. b, bryozoan interior wall lining pagurid living chamber and showing septulae and cuticular traces, × 50. c, frontally-budded autozooids at the free edge of the pagurid aperture, × 50. d, ovicelled zooid (uncalcified frontal area arrowed) and small adventitious avicularia, × 180.

zooid orifice length 0·07–0·09 mm, width 0·05–0·06 mm; interzooidal avicularium rostrum length 0·04–0·05 mm, width 0·07 mm.

Remarks. This new species has been created to accommodate some Recent *Hippoporidra* previously referred to *H. edax* but differing from that species principally in the structure of the interzooidal avicularium. In *H. edax* this has an acuminate rostrum and a doubly constricted pivotal bar, whereas in *H. lusitania* it has an oval-shaped rostrum, with a

transverse long axis, and a simple curved pivotal bar. The adventitious avicularia are generally more rounded in *H. lusitania*, while the ovicells are often less rounded and appear to have a more distally restricted frontal area. *H. lusitania* also has cortical zooids with smaller orifices than those of *H. edax*, so that there is a greater contrast in orifice size between autozooids and cortical zooids within a colony.

Discussion

This brief survey of fossil and living *Hippoporidra* and revision of the type species *H. edax* has some interesting biogeographical implications.

The only species of *Hippoporidra* with a well-documented fossil history is *H. edax*, which had a pan-Atlantic distribution during Miocene and Pliocene times. *H. edax* seems to be restricted to the western side of the Atlantic at the present day. Supposed *H. edax* now living off the western and south-western coasts of the British Isles and the Channel Islands has been shown to be a different species, *H. lusitania* sp. nov. This living population was previously suspected (Hayward & Ryland 1979) to represent the relic of a declining population of *H. edax*, abundant in Europe during the Neogene. Known distributions of *Hippoporidra* in time and space lead to the tentative suggestion that the living eastern Atlantic species of *Hippoporidra, H. lusitania, H. picardi, H. littoralis* and *H. senegambiensis*, arose through allopatric speciation which followed fragmentation of the initially widespread *H. edax* populations.

References

Boardman, R. S. & Cheetham, A. H. 1973. Degrees of colony dominance in stenolaemate and gymnolaemate Bryozoa. *In* Boardman, R. S., Cheetham, A. H. & Oliver, W. A., *Animal colonies* : 121–220. Stroudsburg.

Buge, E. 1957. Les Bryozoaires du Néogène de l'Ouest de la France. *Mém. Mus. natn. Hist. nat. Paris* (C) **6** : 1–436.

—— **& Lecointre, G.** 1962. Une association biologique (symbiose) entre un Bryozoaire et un Pagure dans le Quaternaire du Rio De Oro (Sahara espagnol). *Bull. Soc. géol. Fr.*, Paris, (7) **4** : 555–558.

Busk, G. 1859. A monograph of the fossil Polyzoa of the Crag. xiv + 136 pp., 22 pls. *Palaeontogr. Soc. (Monogr.)*, London.

—— 1861. Description of new or imperfectly known Polyzoa No. I. *Q. Jl microsc. Sci.*, London, (n.s.) **1** : 153–156.

Canu, F. & Bassler, R. S. 1923. North American Later Tertiary and Quaternary Bryozoa. *Bull. U.S. natn. Mus.*, Washington, **125** : 1–302.

—— —— 1927. Classification of the Cheilostomatous Bryozoa. *Proc. U.S. natn. Mus.*, Washington, **69** (14) : 1–42.

—— —— 1928. Fossil and Recent Bryozoa of the Gulf of Mexico Region. *Proc. U.S. natn. Mus.*, Washington, **72** (14) : 1–199.

—— —— 1929. Bryozoa of the Philippine Region. *Bull. U.S. natn. Mus.*, Washington, **100** (9) : 1–685, 94 pls.

Cook, P. L. 1964. Polyzoa from West Africa. Notes on the genera *Hippoporina* Neviani, *Hippoporella* Canu, *Cleidochasma* Harmer and *Hippoporidra* Canu & Bassler (Cheilostomata, Ascophora). *Bull. Br. Mus. nat. Hist.*, London, (Zool.) **12** (1) : 1–35.

—— 1968. Bryozoa (Polyzoa) from the coasts of tropical West Africa. *Atlantide Rep.*, Copenhagen, **10** : 115–262.

—— in press. Bryozoa from Ghana – a preliminary survey. *Annls Mus. r. Afr. Cent.*, Tervuren, (8° Zool.).

Duvergier, J. 1924. Deuxième note sur les Bryozoaires du Néogène de l'Aquitaine. *Act. Soc. linn. Bordeaux* **75** : 145–190.

Håkansson, E. 1973. Mode of growth of the Cupuladriidae (Bryozoa, Cheilostomata). *In* Larwood, G. P., *Living and Fossil Bryozoa* : 287–298. London.

Hayward, P. J. 1978. Systematic and morphological studies on some European species of *Turbicellepora* (Bryozoa, Cheilostomata). *J. nat. Hist.*, London, **12** : 551–590.

—— **& Ryland, J. S.** 1979. British Ascophoran Bryozoans. *Synopses Br. Fauna*, London, **14** : 1–312.

Hincks, T. 1862. A Catalogue of the Zoophytes of South Devon and South Cornwall. *Ann. Mag. nat. Hist.*, London, (3) **9** : 303–310.

—— 1880. *A History of the British Marine Polyzoa.* 601 pp. London.

Lagaaij, R. 1952. The Pliocene Bryozoa of the Low Countries. *Meded. geol. Sticht.*, Maastricht, (C5) **5** : 1–233.

Leriche, M. 1912. Excursion du vendredi 6 Septembre, à Burght et à Anvers. *Bull. Soc. géol. Fr.*, Paris, (4) **12** : 801–807.

Michelin, H. 1841-48. *Iconographie Zoophytologique.* viii + 348 pp., 79 pls. Paris.

Moore, H. B. 1937. Marine fauna of the Isle of Man. *Proc. Lpool biol. Soc.* **50** : 5–293.

Osburn, R. C. 1940. Bryozoa of Porto Rico. *Scient. Surv. P. Rico,* New York, **16** (3) : 321–486.

—— 1952. Bryozoa of the Pacific Coast of America. Part 2, Cheilostomata Ascophora. *Allan Hancock Pacif. Exped.*, Los Angeles, **14** (2) : 271–611.

Pinter Morris, P. A. 1975. A comparative study of decalcification of Mollusca shells by various bryozoans. *Docums Lab. Géol. Fac. Sci. Lyon* (H.S.) **3** (1) : 109–113.

Pohowsky, R. A. 1978. The boring ctenostomate Bryozoa: taxonomy and paleobiology based on cavities in calcareous substrata. *Bull. Am. Paleont.*, Ithaca, **73** (301) : 1–192.

Pouyet, S. 1973. Révision systématique des Cellépores (Bryozoa, Cheilostomata) et des espèces fossiles Européennes. Analyse de quelques populations à Cellépores dans le Néogène du Bassin Rhodanien. *Docums Lab. Géol. Fac. Sci. Lyon* **55** : 1–266.

Roger, J. & Buge, E. 1948. L'association Cellépore–Gastropode dans les faluns de la Touraine. *Bull. Soc. géol. Fr.*, Paris, (5) **17** : 461–470.

Smitt, F. A. 1873. Floridan Bryozoa, Part 2. *K. svenska VetenskAkad. Handl.*, Stockholm, **9** (4) : 3–83.

Ulrich, E. O. & Bassler, R. S. 1904. Systematic Paleontology (of Maryland). Bryozoa. *Maryland Geological Survey, Miocene* : 404–429. Baltimore.

Vigneaux, M. 1949. Révision des Bryozoaires Néogènes du Bassin d'Aquitaine et essai de classification. *Mém. Soc. géol. Fr.*, Paris, (n.s.) **28** : 1–55.

Wood, S. V. 1872–74. Supplement to the Mollusca from the Crag: being descriptions of additional species, and remarks on species previously described. xxxi + 231 pp., 10 pls. *Palaeontogr. Soc. (Monogr.)*, London.